

Evolutionary aspects of mutualistic associations between fungi and photosynthetic organisms

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Introduction

At the outset, it is necessary to delimit precisely the concept of mutualism, the taxonomic limits encompassed by the organisms discussed in this chapter and the nature of the symbioses considered. 'Symbiosis' is used in its literal meaning of 'living together', with no overtones of time or nature of contact (Lewis, 1985).

Notwithstanding the problems of quantitatively assessing the fitness of fungal individuals, mutualism is defined as the outcome of those symbioses in which the fitness of *both* symbionts is increased as a result of the association (Law & Lewis, 1983; Lewis, 1985). Following Margulis & Schwartz (1982), the fungi are limited to the Zygo-, Asco- and Basidiomycota (= -mycotina) and their imperfect forms. The autotrophs are either prokaryotic cyanobacteria or eukaryotic protocistan algae (principally Chlorophyta) and land plants (Bryophyta and Tracheophyta). Table 11.1 lists the three kinds of mutualistic association between fungi and photosynthetic organisms to be considered. The reasons for regarding these as mutualistic are set out below. It must be stressed that the nature of the outcome of a symbiosis (see Lewis, 1985 for the continua involved) is important because selective forces act differently on the symbionts depending on this outcome (Law & Lewis, 1983; Law, 1985).

Mycorrhizas

The mutualistic mycorrhizas

There are good reasons for substituting the now rightly defunct classification of mycorrhizas into ecto- and endo-trophic kinds with another dichotomy. This is between those where net movement of carbon (especially as carbohydrate) has been demonstrated or can be reliably

inferred to be *usually* from plant to fungus, and those where the opposite obtains (Fig. 11.1). Only the former kinds are mutualistic (Table 11.1). The qualification 'usually' is needed because of the demonstration of the marked movement of carbon between plants of the same or different species when connected by ectomycorrhizal or V-A mycorrhizal fungi (Brownlee *et al.*, 1983; Francis & Read, 1984; Finlay & Read, 1986).

To the eight kinds of mycorrhiza noted in Fig. 11.1 may be added those found in *Pisonia grandis* (Ashford & Allaway, 1982, 1985) and *Carex* species (Haselwandter & Read, 1982). The direction of net flux of carbon in these associations has not been determined (Table 11.2) but it could be from fungus to plant (Lewis, 1986). Although the description, Nyctaginaceous, has been applied to mycorrhizas of *Pisonia* (Lewis, 1986), it is not yet known whether their characteristic transfer cells consistently occur in the ectomycorrhizas of other genera of the Nyctaginaceae, e.g. those of *Neea* species (see Alexander & Hogberg, 1986). The occurrence of transfer cells may be a generic rather than a familial character.

Mycorrhizal types below the dotted line in Fig. 11.1 and in the right-hand column of Table 11.2 are classified as agonistic (+/-) (Lewis, 1985) because the fungi supply both carbon *and* mineral nutrients to the plant and, as yet, there is no clear evidence that their own fitness is increased by symbiosis. As such, these mycorrhizas are beyond the scope of this chapter, except with regard to their evolutionary relationships to mutualistic kinds. The five kinds of mycorrhiza placed above the line in Fig. 11.1 and in the mutualistic column of Table 11.2 are delimited as types I, II and III. Their general biological features have most recently been considered by Harley & Smith (1983) and Gianinazzi-Pearson &

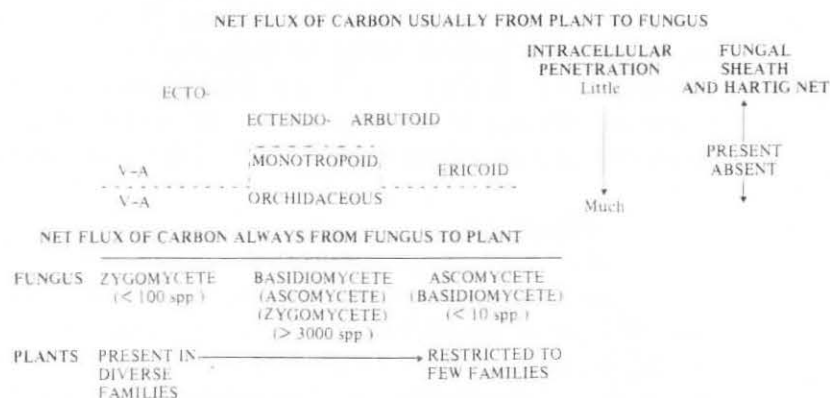


Fig. 11.1. Characteristics of the principal kinds of mycorrhiza.

Table 11.1. *Mutualistic symbioses between fungi and photosynthetic organisms*

Photosynthetic organisms	Symbioses
A. Whole organism	
(i) Cyanobacteria	Lichens
(ii) Algae	Lichens
B. Photosynthetic tissue of land plants	Endophytic symbioses
C. Non-photosynthetic tissue of land plants	Some mycorrhizas

Table 11.2. *Summary of types of mycorrhiza in relation to net flux of carbon between the symbionts (cf. Fig. 11.1)*

Mycorrhizal type	Net carbon flux	
	Plant to fungus (mutualistic)	Fungus to plant (agonistic)
I V - A	*	*
Ecto	*	
II {	Ectendo	
	Arbutoid	
	Monotropoid	*
Nyctaginaceous		?
III Ericoid	*	
IV Orchidaceous		*
IV? Cyperaceous		?

Gianinazzi (1986) whilst their ecological features are summarised in Fig. 11.2. These features will now be examined in an attempt to delimit the selective forces controlling evolution of the three main types of mycorrhiza. An alternative approach via strategy theory (Grime, 1974; Cooke & Whipps, Chapter 9) deserves attention but has not yet been attempted.

Origin and evolution of Type I (vesicular - arbuscular) mycorrhizas

Vesicular - arbuscular (V - A) mycorrhizas, the most widespread extant fungal symbioses, involve only six zygomycetous genera and perhaps 200 species (Trappe, 1982; Trappe & Schenck, 1982). They may represent an isolated relict taxon (Law & Lewis, 1983). All appear to

be obligately dependent on plants as sources of carbon. Although both Bryophyta and Tracheophyta possess V – A mycorrhiza, only the latter will be considered because the early history of the former is so sparse and the same argument would, in any case, apply.

The adaptations necessary to transform a characean green alga into a land plant have been discussed by Raven (1977, 1984, 1985, 1986). The observation that early vascular land plants had Type I mycorrhizas (see Harley, 1969; Nicolson, 1975; Pirozynski, 1976) led Pirozynski & Malloch (1975) to conclude that their very origin was intimately dependent on the mycorrhizal habit (see also Malloch, Pirozynski & Raven, 1980; Raven, 1977; Raven, Smith & Smith, 1978; Pirozynski, 1981). The first macrofossils of land plants (*Cooksonia*), some of which are clearly vascular, are Silurian (Edwards & Fanning, 1985) but earlier Ordovician microfossils have also been attributed to a land flora (Gray, 1985). These early land plants would have been subjected to precisely the same selective forces that extant plants currently respond to by association with fungal partners: viz., acquisition of minerals and water, maintenance of compatible acid – base balance and exclusion of toxic elements (Read, 1984; Raven *et al.*, 1978). Furthermore, it has been argued that lignification was primarily a defence reaction, only later exploited in vascular tissue and

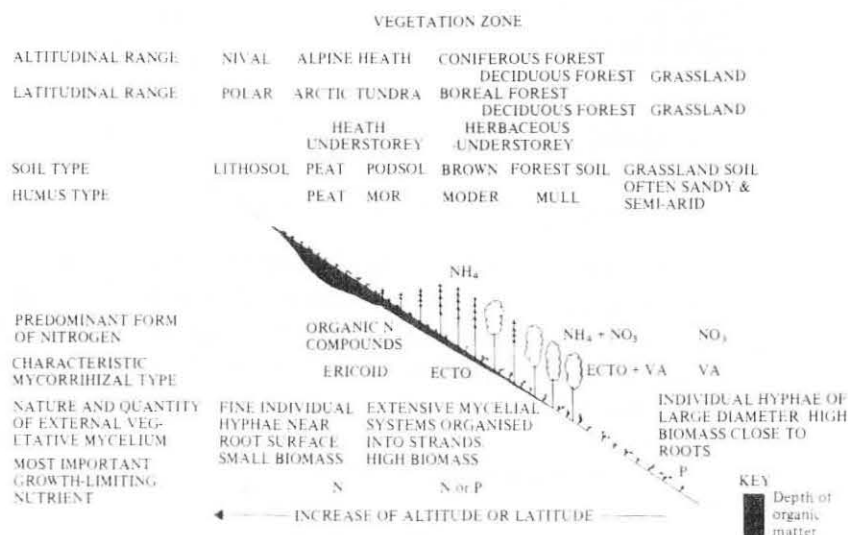


Fig. 11.2. Diagrammatic presentation of the postulated relationship between latitude or altitude, climate, soil and mycorrhizal type, and development of the vegetative mycelium associated with mycorrhizas. (Slightly modified, with permission, from Read, 1984.)

still later for support (Raven, 1977, 1984). Fungal infection of the precursor charophyte may therefore have stimulated lignification and been responsible for acquisition of resources from soil.

The suggestion that the first land plants were obligately mycorrhizal is reinforced by the fact that even early Devonian plants, e.g. *Rhynia* and *Asteroxylon*, had no roots. Unless elements were present in Ordovician, Silurian and Devonian soils in much greater concentrations than in extant soils, it is likely that phosphorus would often have been growth limiting (see Fig. 11.2). Not only is phosphorus, as phosphate, present in soil solutions at concentrations some two to three orders of magnitude lower than other macro-nutrients (Epstein, 1972) but it is extremely immobile (Nye & Tinker, 1977). Land plants need to grow towards phosphate rather than wait for it to diffuse to them! Clearly, the early vascular plants achieved this via mycorrhizas, a situation which, 400 million years later, persists in over two hundred thousand species.

During the 120 million years of the Devonian and Carboniferous, vascular plants evolved in several directions by increase of size, to about 40 m, and by becoming woody (Raven, 1986). Before considering the origin of the ectomycorrhizal habit, the following features need to be emphasised. Firstly, if the gametophytes of some early trimerophytes, pteridophytes and lycopsids were similar to those of *Psilotum* and some extant ferns and clubmosses (see Harley, 1969), they were heterotrophic and agonistically dependent on their type I mycorrhizal associates. Secondly, the Carboniferous is named after its massive deposits of coal, much derived from wood.

Origin and evolution of Type II mycorrhizas

Extant ectomycorrhizas are characteristic of mull and moder soils (Fig. 11.2). However, although such soils had developed by the early Carboniferous (Wright, 1985), the ectomycorrhizal habit probably had not, only really coming into its own during the Cretaceous (Pirozynski & Malloch, 1975; Malloch *et al.*, 1980). Nonetheless, it was during the Carboniferous that the stage was set for these symbioses. The massive deposits of carbon in this and later Eras were due to low rates of decay (Schopf, 1952). This suggests either lack of appropriate degradative organisms, or deficiency of oxygen, the co-substrate for rapid decay, or both.

White rot basidiomycetes degrade lignin most rapidly (Reddy, 1984; see also Whalley & Edwards, Chapter 28, for xylariaceous ascomycetes). As Dennis (1970) demonstrated clamp connections on hyphae in wood of a

Carboniferous fern, these basidiomycetes were thought to have originated in the Carboniferous itself (Pirozynski, 1976). However, Stubblefield, Taylor & Beck (1985) have now provided convincing evidence for the existence of wood-inhabiting fungi, likely to be basidiomycetes, in the late Devonian, so appropriate organisms for rapid decay of wood existed at the start of the Carboniferous. Attention must therefore be focussed on the availability of oxygen.

While much deposition of carbon undoubtedly took place under acidic, waterlogged conditions, it is not clear what the precise atmospheric concentration of oxygen was during the period when the basidiomycetes emerged. To understand the relevance of this, it is necessary to digress to the mechanism by which lignin is degraded. This is because the process is a highly oxidative one and, in the best-studied organism, *Phanerochaete chrysosporium*, which may not be representative of the full range of ligninolytic fungi, occurs optimally at 40 – 60% O₂. Rates at 100% O₂ are two to three-fold higher than in air (Kirk & Fenn, 1982). The precise role of oxygen is not clear. The 'ligninase' initiating breakdown is an extracellular, haem-containing peroxidase which, after reaction with hydrogen peroxide, oxidises lignin, thereby generating cationic free radicals. These, in turn, cause further degeneration of the polymer by a chain reaction (J.M. Palmer, personal communication; see Paterson & Lundquist, 1985). As 'ligninase' may also catalyse polymerisation of fragments, stabilisation of these by oxidations catalysed by phenol oxidases utilising molecular oxygen (e.g. laccase and polyphenol oxidases) may be an important adjunct to the initial degradative steps. The oxidases, which also catalyse further degradation, have a low affinity for oxygen so that the network of reactions, as well as the synthesis of the enzymes themselves, is highly aerobic. Also, since lignin occurs in wood as lignocellulose, enzymes which break down cellulose, including a cellobiose:quinone oxidoreductase, are intimately concerned with the overall degradation. Lastly, the ability to degrade lignin is a feature of secondary metabolism, a metabolic phase induced by low availability of carbon, sulphur or, especially, nitrogen (Reddy, 1984), a situation especially relevant in naturally N-poor wood.

The history of changes in atmospheric oxygen concentration in the Phanerozoic is much disputed (Holland, 1984; Raven, 1985). Although much evidence is geochemical, three biologically related phenomena do set limits; the concurrent appearance of flying insects and fossil charcoal in the Devonian and the bulkiness of plant tissues in the late Carboniferous (Raven, 1985, 1986). Taken together, they suggest that atmospheric

oxygen concentration was not less than 0.3 – 0.6 of the extant value when basidiomycetes first appeared. For further details and alternatives, see Broecker (1970), Walker (1977), Hart (1978), Cope & Chaloner (1980, 1981), Clark & Russell (1981), Holland (1984) and Holland, Laza & McCaffrey (1986). One alternative view (Walker, 1977), envisages a concentration during the Carboniferous much higher than at present. If confirmed, this might account for the low affinities of phenol oxidases for molecular oxygen in that these enzymes first evolved in an oxygen-rich environment.

From the above, it is clear that basidiomycetes capable of destroying wood either as saprotrophs or necrotrophs were present by the start of the Carboniferous. As such, they may have posed a threat to woody plants, perhaps thereby acting as an important selective force in the origins of sinapyl-rich (angiospermous) lignin and, indeed, of the re-emergence of the herbaceous (low-lignin) habit among angiosperms. [See Rayner (1986) for a discussion of factors affecting the *internal* concentration of oxygen in woody tissues. He has also pointed out (personal communication) that, with regard to ligninolysis and mycorrhizal infection, concentration of oxygen around roots in the soil environment is more important than that around shoots in the air.] Despite this threat, however, basidiomycetes were not 'tamed' into the ectomycorrhizal state until much later. Fossils of Pinaceae, the principal extant ectomycorrhizal gymnospermous taxon, do not appear until the late Triassic, and *Pinus* itself not until the Cretaceous, contemporary with ectomycorrhizal angiospermous taxa (see Malloch *et al.*, 1980).

As ligninolysis is a feature of secondary metabolism, it follows that maintenance of potentially ligninolytic fungi in a primary metabolic state will suppress this potential. This could have been achieved by absorption of nitrogen and phosphorus from organic soils, concomitant with carbon from a woody host in a biotrophic manner. Ectomycorrhizal utilisation of organic nitrogen is discussed by Abuzinadah, Finlay & Read (1986) and Abuzinadah & Read (1986a & b). Geological and physiological considerations therefore suggest that ectomycorrhizal biotrophy is derived from the saprotrophic/necrotrophic direction (cf. Lewis, 1973). It is also likely that ectomycorrhizal plants are geologically more recent than their fungi from the fact that fungal genera are common to both Northern and Southern hemisphere plants (Trappe, 1962). This is consistent with establishment of the fungi before the split of the Pangean land mass (Pirozynski, 1981; cf. Miller & Watling, Chapter 29) and with the propensity of ectomycorrhizal symbioses to be characteristic of the higher

latitudes (Fig. 11.2). However, the greater potential for dispersal exhibited by fungal spores should not be overlooked. The taxonomic and phylogenetic relationships of wood-destroying and ectomycorrhizal basidiomycetes are discussed by Watling (1982), Miller & Watling (Chapter 29), and Kuhner (1984).

The above discussion is not, however, meant to imply that the dichotomy, wood-destroying vs. ectomycorrhizal, is absolute. There is much evidence for a continuum between the two extremes as has been reinforced by recent evidence of utilisation by ectomycorrhizal fungi of lignin, lignocellulose and cellulose from Trojanowski, Haider & Hüttermann (1984) who cite earlier studies to support this view.

From the compilations of Malloch *et al.* (1980) and Harley & Smith (1983), supplemented by more recent studies of tropical and Australian species (Warcup & McGee, 1983; Alexander, 1986; Alexander & Hogberg, 1986), the ectomycorrhizal habit clearly occurs widely in taxonomically unrelated orders of angiosperms (including herbaceous species) many of which only date to late Cretaceous or even early (Paleogene) Tertiary. The fungi are, therefore, probably still extending their range of angiospermous hosts.

Like V – A mycorrhizal fungi, ectomycorrhizal species exploit their hosts for carbon whereas the plants gain more varied and extensive physiological attributes, notably an ability to obtain nitrogen from sources not otherwise available (Abuzinadah *et al.*, 1986; Abuzinadah & Read, 1986a & b). The fungi also provide water, particularly where seasonal aridity occurs (Alexander, 1986). Indeed, K. A. Pirozynski and D. C. Smith (personal communication) link the development of the ectomycorrhizal habit to the onset of pronounced climatic fluctuations. This is in line with the relationship to plate tectonic events already mentioned.

Origin and evolution of Type III (Ericoid) mycorrhizas

Unlike mycorrhizas considered in the previous two sections, the type III, ericoid, kind is taxonomically restricted to a close-knit group of families in the Ericales (Malloch *et al.*, 1980; Read, 1983). Their overall geographical and ecological range is indicated in Fig. 11.2. Ericoid mycorrhizal fungi must not only be able to utilise complex sources of nitrogen and phosphorus and tolerate high concentrations of elements, such as manganese and aluminium, more soluble at low pH, but also must be well adapted to the polyphenolic environment of mor humus. Moreover, since ericaceous plants are often rich in phenolic glycosides (Franz, 1982), any tolerance of soil phenolics by fungi with access to complex

nitrogen and phosphorus compounds would preadapt them to becoming mutualistic endophytes. These attributes are found in the ascomycetous *Hymenoscyphus* (= *Pezizella*) *ericae*, the imperfect *Oidiodendron* species and related strains and, possibly, the basidiomycetous *Clavaria argillacea* (Englander, 1982; Read, 1983; Dalpé, 1983; Miller & Watling, Chapter 29). This mutualistic symbiosis is, however, geologically recent, fossil records of the Ericaceae dating back only to the late Eocene whereas the Epacridaceae, from its biogeographical distribution, is possibly Cretaceous (Raven & Axelrod, 1974; K. A. Pirozynski, personal communication). This recent origin probably means that there has been insufficient time for any agonistic versions to develop.

Evolutionary relationships between mutualistic and agonistic mycorrhizas

Implicit in the last sentence is that for type I and type II mycorrhizas there is an evolutionary relationship between mutualism and agonism. Furthermore, if the initial vascular plants were mycorrhizal, the non-mycorrhizal condition is necessarily derived. The most important interactive selective forces bringing about the mutualistic condition consequent upon the sharing of resources are improvement of acquisition of carbon by the fungi, and of other resources by the plants, plus ease of infection of plants by the fungi.

Conservation of carbon by the plant appears to be important in the evolution both of agonistic mycorrhizas and the non-mycorrhizal condition. In agonism, carbon is not only conserved but is derived partially or wholly from fungi in a hemibiotrophic manner, whereby biotrophy is superseded by necrotrophy. Hence, the fungi lose their ability to derive resources from plants whilst the latter retain their susceptibility to infection. Three kinds of fungi are involved (Fig. 11.1), (a) typical V – A endophytes in heterotrophic archegoniate gametophytes and Gentianaceae, (b) typical ectomycorrhizal endophytes in *Monotropa* and its allies, and in some orchids and (c) facultatively necrotrophic fungi (e.g. *Rhizoctonia* and *Armillaria*) (Harley, 1969; Harley & Smith, 1983). The last group appears to be the result of direct 'taming' of pathogens, there being no mutualistic equivalent. To exist in the non-mycorrhizal condition, plants must be able to acquire resources, especially phosphate, independently of fungi. This can be achieved by restriction to nutrient-rich, disturbed habitats and by extrusion of protons into the rhizosphere, so solubilising otherwise unavailable sources of phosphate (Grinsted, *et al.*, 1982; Hedley, Nye & White, 1982, 1983; Hedley, White & Nye, 1982).

At the same time, fungi are excluded by increased resistance to infection.

Conservation of carbon can be achieved by synthesis of carbohydrates which are either not readily available as carbon sources to invading organisms or which, more effectively, are actually toxic. Orders considered to be evolutionarily advanced among both di- and monocotyledons contain a range of soluble sugars. In these, the basic molecule of sucrose is extended by addition of units of fructose, galactose or glucose to yield the various sucrosyl - fructans and sucrosyl - galactans and the single sucrosyl - glucan, gentianose (Lewis, 1984). Fructans are not toxic to fungi as shown by the occurrence of V - A mycorrhizas in many species of Asterales and Poales. However, Lewis (1986) has speculated that sucrosyl - galactans and gentianose may give rise to reducing disaccharides (melibiose and gentiobiose) which, by acting as agents capable of sequestering phosphate, could alter permeability of membranes as do other analogues of glucose (Herold & Lewis, 1977). Indeed, one function of the extracellular, wall-bound invertase of vascular plants (ap Rees, 1984) could be the hydrolysis of non-toxic, non-reducing trisaccharides such as raffinose and gentianose to protective, toxic reducing disaccharides. Thus, depending on toxicity and concentration of such sugars, potentially pathogenic or mutualistic fungi could either be prevented from infecting completely or be overcome after infection. Fungi in the latter situation would be induced to release nutrients including carbon compounds to plants over a substantial period, the agonistic mycorrhizal situation. This testable hypothesis should be viewed in the light of the effects of exogenous mannose on release of electrolytes from leaf discs of spinach beet over a period of days (Herold, 1978).

Here, it is relevant that the taxonomically isolated, largely non-mycorrhizal order, the Caryophyllales, includes families such as the Caryophyllaceae and Chenopodiaceae which store sucrosyl - galactans. Also, within the order is the Nyctaginaceae with its peculiar mycorrhizas. Whether these are related to the occurrence of peculiar sugars is not yet known (Lewis, 1986). Mycorrhizas of the Gentianaceae, some genera of which contain gentianose and gentiobiose, are also unusual (Jacquelinet-Jeamougin & Gianinazzi-Pearson, 1983; McGee, 1985).

Another way of sequestering sugars is as phenolic and other glycosides. Although over 50 kinds of disaccharide exist in various glycosides (Avigad, 1982), a role for this diversity has yet to be suggested. Could they be anti-fungal in the manner suggested above for more familiar disaccharides? With their extensive range of mycorrhizal types, the Ericales would be an ideal order in which to investigate these possible interrelationships.

Endophytic symbioses between fungi and the aerial parts of plants

The concept that symbioses between endophytic fungi and shoots, previously often referred to as symptomless parasitism, are both abundant and mutualistic is rapidly gaining ground following work by Carroll, Clay and Müller (e.g. Carroll, 1984; Carroll & Carroll, 1978; Clay, 1984; Luginbühl & Müller, 1980a & b; Petrini & Dreyfus, 1981; Petrini, Stone & Carroll, 1982; Riesen & Sieber, 1985).

This upsurge in interest warrants a more concise terminology for these associations which I propose to call 'mycophylla' (singular: 'mycophyllon'; adjective: 'mycophyllous'). Just as mycorrhizas also encompass infection of rhizoids and rhizomes, mycophylla would include infections of both aerial stems and leaves. In line with the all-embracing definition of mycorrhizas of Harley (1959), mycophylla are associations of fungi and photosynthetic organs constant in structure and development and consistently present and functional under natural conditions. Consequently, infections of heterotrophic archegoniate gametophytes remain as mycorrhizas whereas those of photosynthetic gametophytes become mycophylla.

Bradshaw (1959) showed that infections of *Agrostis capillaris* (= *A. tenuis*) by *Epichloe typhina* could be '... of advantage to plants growing under conditions where vegetative growth is important ...'. Infection of other grasses by species from other clavicipitaceous genera (*Atkinsonella*, *Balansia*) and the anamorph of *Epichloe*, *Acremonium*, also enhance vegetative vigour (see Clay, 1986). This phenomenon was investigated experimentally by Clay (1984) who showed that infected ramets had higher rates of survival and growth, but lower reproductive capacities, than uninfected ones. This increased fitness of ramets at the expense of production of genets has been demonstrated to be due to production of alkaloids in infected tissues which deter both invertebrate and vertebrate predators. Work in New Zealand, reviewed by Clay (1986), has been especially revealing. Movement of photosynthetically fixed carbon from grass to fungus has been demonstrated by Thrower & Lewis (1973) for the *Agrostis stolonifera*/*E. typhina* combination. The fungi may well be obligate biotrophs in the sense of Lewis (1973). It would be of interest to determine whether the mycophylla of leafy liverworts (Pocock & Duckett, 1985) are less palatable to predators than axenically raised gametophytes.

It seems probable that mycophylla arose early in the history of the land flora in response to predatory pressure and may even pre-date vascular plants. As noted above, Gray (1985) believes that a bryophyte-like flora existed in the Ordovician and, certainly, endophytic hyphae were present in the aerial parts of plants from the Devonian onwards (Pirozynski,

1976). Whether the outcome of these associations was mutualistic or not cannot, of course, be assessed from the fossil record.

Lichens

Almost 50% of ascomycetous species (ca. 13 500) are associated with cyanobacteria, Chlorophyta (or both) or, in a few cases, eukaryotic algae from other phyla as lichens (Hawksworth & Hill, 1984). There are also a few basidiolichens (less than 2% of all lichens). In terms of the outcome of these symbioses, most lichens are clearly mutualistic for the associations are ecologically obligate, i.e. the fitness of both partners approaches zero when they are not together.

Pirozynski (1976) asserted that ascomycetes probably originated in the Mesozoic but more recent evidence (Sherwood-Pike & Gray, 1985) indicates that this group of fungi is much more ancient (Silurian). A land flora which included septate fungi was therefore probably contemporaneous with the origin of vascular plants. Indeed, it is possible that these vascular plants emerged from a soil surface encrusted and stabilised by cyanobacteria, algae and lichens (cf. Wright, 1985; and Schulten, 1985). Biogeographical arguments also suggest that lichens are pre-Mesozoic in origin (e.g. Sipman, 1983; Tehler, 1983; Hawksworth & Hill, 1984).

Ahmadjian (1970) has discussed the origin and evolution of lichens, Barrett (1983) co-evolutionary aspects and Smith, Muscatine & Lewis (1969) pointed out some similarities of the physiology of the Capnodiaceae and green-algal lichens. It seems probable that, as for mycorrhizas, there are several different kinds of lichen with polyphyletic origins within the ascomycetes (e.g. see Honegger, 1986 for a range of haustorial types in trebouxoid lichens). The taxonomic positions and morphological versatility of the fungi involved are well documented but a closer integration with the ecology of lichens as a group and the relationships of their fungi to free-living and agonistic relatives as well as to those showing other mutualistic modes is necessary to understand their evolution.

Epilogue

The above discussion has necessarily been selective in its approach and, often, speculative in its outcome. A major omission has been any quantitative or theoretical consideration of the costs and benefits involved (see Keeler, 1985). Assessment of fitness of fungi under natural conditions is especially difficult owing to their indeterminate growth form (cf. Rayner & Coates, Chapter 8; Caten, Chapter 15). Linked with this is the nature and frequency of sexual reproduction and other methods of

generating genetic change. Law & Lewis (1983) and Law (1985) have stressed the preponderance of asexual reproduction among intracellular mutualistic symbionts including the fungi of V – A and ericoid mycorrhizas. Does the trend towards asexuality of the fungi in mycophyllous associations (e.g. the *Epichloe/Acremonium* relationship) indicate a relatively recent origin of this particular kind of association? How does the frequently observed suppression of sex in the host plant affect the evolution of these symbioses? The suggestion that soluble carbohydrates are involved in the origin of both agonistic mycorrhizas and the non-mycorrhizal condition is testable in so far as the study of the effects of sundry reducing disaccharides on the permeability of fungal membranes is amenable to experiment although, as always, interpretation of results in an evolutionary context should be made with care.

It is evident that there are many kinds of mycorrhizas. This should alert all to the probability of diverse kinds of mycophylla and lichens. In this way, broad generalisations should be avoided and, as is implicit in the above discussion, solutions to evolutionary enigmas will only emerge from inter-disciplinary approaches to particular problems. Evidence from taxonomy, anatomy, morphology, physiology and biochemistry must be integrated with that from ecology, biogeography, paleoclimatology, paleopedology and plate tectonics.

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